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COEXISTENCE OF COMPETING POPULATIONS ALONG AN ENVIRONMENTAL GRADIENT: A SIMULATION STUDY[1]

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Abstract. It has been repeatedly suggested by several kinds of competition models (island models, diffusion models and simulations of local dynamics) that spatially limited dispersion and local competition stabilize the regional coexistence of competing populations. Using a Monte Carlo simulation model, this work demonstrates that local dynamics alone is insufficient to allow stable coexistence of similar species: it is the environmental heterogeneity inherent in island models and most of the simulations that has the stabilizing effect. Increasing spatial inhomogeneity by the introduction of an environmental gradient and the corresponding response curves results in an increased tendency for stable regional coexistence of two annual plant populations.

Introduction

In considering coexistence problems, an increasing number of recent theoretical studies on competition emphasize the importance of local dynamics as a possible source of stability. In these models it is supposed that the topographical range within which population dynamical features can be effective is limited. Neighborhood relations are taken into account regarding dispersal and competition; that is, seeds or propagules cannot get to any distance with equal ease, and the competitive effect exerted by an individual upon another diminishes as the distance between them increases. These are essential and plausible modifications to the classical models, e.g. of the Lotka-Volterra type, which postulate that the intensity of population interactions is a function of the population abundances alone (cf. Strobek 1973, May 1976, Begon *et al.* 1986). Neighborhood effects are especially important factors in the population dynamics of plants or sessile animals, although it is obvious that on a larger topographical scale the "zone of influence" for even extremely mobile animal populations such as migratory birds is more or less restricted as well.

It is generally concluded that the outcome of competition is more likely to be coexistence if the neighborhood relations are considered than if not. This conclusion has been drawn mainly from three different kinds of competition models. These models use different mathematical tools, but they have in common the assumptions of limited dispersion of propagules, and local (neighborhood) competition:

a) Island or "patchy environment" models, supposing that the habitat within which competition takes place is fragmented, and dispersion among patches is relatively low (De Angelis *et al.* 1978, Hanski 1983, Levin 1986, Pacala 1986 and 1987, Seno 1988).

b) Simulations of local dynamics, modeling population interactions within grids. Most of these employ Monte-Carlo methods (Weiner and Conte 1981, Karlson and Jackson 1981, Czárán 1984, Crawley and May 1987).

c) Diffusion models using partial differential equations (Shigesada *et al.* 1979, Okubo 1980, Kohyama 1987).

In the island models, there is an inherent assumption of environmental heterogeneity: the islands (patches) are inhabitable, the areas around them are hostile to the populations considered. The simulation models are similar to the island models in that they define a grid of sites, each of which can be thought of as a single island. Although there is no "ocean" around the sites (as they are surrounded by other sites), their boundary lines represent singularities in environmental conditions; that is, such models also presuppose environmental heterogeneity. The diffusion models do not necessarily contain such built-in assumptions of the inhomogeneity or heterogeneity of the environment: these must be specified by introducing environmental gradients into the equations. Shigesada *et al.* (1979) show that it is the presence of an environmental gradient that stabilizes the coexistence of two similar competing species in a diffusion model. In short, all the models incorporating the local character of population interactions consider environmental heterogeneity as well; otherwise (as in diffusion models without gradients), no coexistence follows. All this amounts to the

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hypothesis that it is not local dynamics alone that enables the coexistence of competing species: a certain level of environmental inhomogeneity (or heterogeneity) is necessary to stabilize the effect of limited dispersion and local competition. The aim of this work is to support this hypothesis by means of a Monte-Carlo simulation model, which works in discrete time and space. Although the model has been developed for annual plant populations, its results may be adapted to more general cases, assuming a limit for the distance an individual can move away from its birthsplace through its lifetime.

I. Model situation

I.1. Population growth and dispersion

In this study, the arena for two competing annual plant populations is a rectangular grid composed of 51×25 square units. The units are sites, each of which is supposed to be large enough to support no more than k plant individuals, regardless of their species identity. (That is, k stands for a kind of "local carrying capacity", which is the same for both species. The latter assumption might be interpreted as considering "similar" species, regarding resource demand and size). The local carrying capacities are related to the spatial resolution level in a given set of parameter values in the model: increasing the k values (with all other parameters kept constant) mean simulating the same process on a larger topographical scale and at a coarser resolution level.

Time is measured in discrete units (e.g., years). In time unit 0, a given number N_i (0) of individuals of species i are present in the grid, in random positions. For time t+1, an individual of species i at a given site in time t produces f_i propagules, scatters them around itself, and dies. Each offspring is dispersed into a neighbouring site with a probability of p_i, and remains in the site of its parent with probability 1-p_i. It is equally easy to reach any of the 8 neighbouring sites from a site inside the grid, that is, the grid is isotropic regarding propagule dispersion. Propagules scattered outside the grid (from marginal sites) can either get back (cf. Section II.1), or be lost (cf. Section II.2).

I.2. Competition

The mechanism described above generates a pattern of propagules in the grid, which is then modified by competition. If a site contains more then k propagules, their number is reduced to k by an iterative process as follows:

Let the number of individuals of population 1 in site m be n_{1m}, and if

$n_{1m}+n_{2m} > k$, then let

$$c_{1m} = n_{1m}\,(n_{1m}+A_{12}\cdot n_{2m})$$

$$c_{2m} = n_{2m}\,(n_{2m}+l_{21}\cdot n_{1m})$$

where A_{ij}—s are the interspecific competition coefficients, measuring the competitive effect on population i of an individual from population j, as compared to one from population i. This interpretation of the competition coefficient is similar to the one applying to the classical Lotka-Volterra models, and thus differs from that based on resource exploitation only. It focuses on the ability of one species to exclude the other, regardless the exact mechanism of exclusion. This kind of indirect competition is often called "interference competition" (see e.g. Pianka 1976). It allows the carrying capacities to vary independently from the competition coefficients, which in our case means that the carrying capacities (k—s) can be equal for the two populations, without the interspecific competition coefficients (a_{ij}—s) necessarily being all equal. Note that $a_{ii} = 1.0$ for both populations, which follows naturally from the above definition of the competition coefficients.

Then, n_{1m} is reduced by 1, and n_{2m} remains the same with a probability

$$P_{1m} = c_{1m} \,/\, (c_{1m}+c_{2m})$$

The complementary event occurs with a probability

$$P_{2m} = c_{2m} \,/\, (c_{1m}+c_{2m})$$

Thus, with $P_{1m}+P_{2m} = 1.0$, one step of the iteration always reduces the total number of individuals in site m by 1 and only 1 (if it exceeds k). Iteration is continued until

$$n_{1m}+n_{2m} = k.$$

In a sense, this definition of the mechanism of local (within site) competition is a stochastic equivalent of that of the Lotka-Volterra model (cf. the simulation model of Weiner and Conte 1981). It will be shown in Section II that without environmental inhomogeneity introduced, the local behaviour of the model is very similar to that of the Lotka-Volterra competition equations in some respects.

I.3. Response curves

Suppose that the grid lies parallel to a gradient of a non-resource type, i.e., conditioning environmental factor that the populations growing there can respond to (e.g. temperature, soil humidity, salinity etc.). Let this factor affect the potential competitive abilities of the populations (a_{12} and a_{21}) according to Gaussian shaped optimum curves, with a given distance of means (d), and the same deviation parameters (σ) for both po-

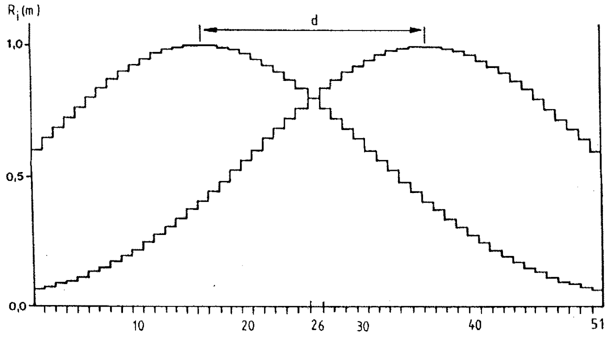

Fig. 1. Shape and position of the response curves along the grid.

pulations present in the grid. For simplicity, the environmental gradient is assumed to be linear. In this way the values of the response curves can be directly assigned to the columns of the grid, as shown in Fig. 1. Thus, sites within the same row of the grid differ from each other, but those within the same column are supposed to be identical environmentally.

The optimum points of the response cruves, M_1 and M_2, are $\mp d/2$ sites away from the central sites of the grid (which are the 26th sites in each row). The optimum value of the curves is 1.0, meaning that at optimum conditions the species in question can show its full competitive strength against other species. Thus,

$$M_1 = 26 - d/2$$

$$M_2 = 26 + d/2$$

and in all sites belonging to the ℓth column of the grid,

$$R_i(\ell) = \exp \frac{-(\ell - M_i)^2}{2\sigma^2} .$$

Towards the suboptimal states, the realized competition coefficients (A_{ij}—s) decrease proportionally to the values of the response curves (see Fig. 1):

$$A_{21}(\ell) = a_{21} * R_1(\ell)$$

$$A_{12}(\ell) = a_{12} * R_2(\ell)$$

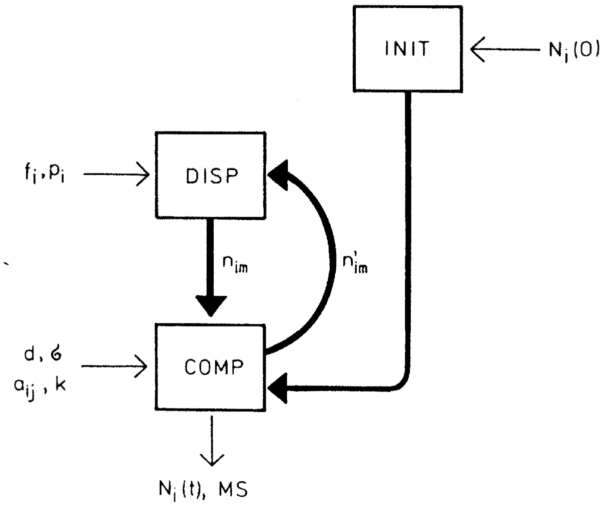

Fig. 2. Schematic flow diagram of the simulation program.
Legend:
INIT: Initializing module
DISP: Dispersal module
COMP: Competition module

Again, this interpretation of "response curves" is not exactly the conventional one, since it refers not directly to the more or less easily detectable birth- or death-response, but to some not so readily measurable (and here implicit) vitality-responses, leading to changes in competitive strength, and thus to indirect changes in the numbers of births and deaths. However, supposing that the "optimum state" on an environmental gradient for a population is the same, or at least very close, for births, deaths and competitive abilities (which is not an unreasonable assumption), taking also direct birth- and death responses into account would only reinforce the effect of the competitive response. As preliminary simulations show, by incorporating the direct responses as well, the final state does not change qualitatively, but the time taken to reach it may differ. The case when the optimum points on the gradient are diffe-

Table 1. List of all variables and parameters used in the model; Fig. 2. depicts the flow diagram of the simulation program. It was written in BASIC, compiled and run on an IBM PC AT machine.

PARAMETER OR VARIABLE	DEFINITION
a_{12}, a_{21}	Interspecific competition coefficients ($a_{11} = a_{22} = 1.0$)
k	Local carrying capacity; # of individuals supported by a site
N_1, N_2	Regional abundances; total # of individuals within the whole grid
n_{1m}, n_{2m}	Local abundances; # of individuals within site m
f_1, f_2	Fecundities; # of offsprings produced per time unit
p_1, p_2	Dispersal parameters; chance of propagule dispersion from site of parent individual
d	Distance of response curves; optimum points (M_1 and M_2) at 26 +— d/2
σ	Steepness of response curves; standard deviation of the Gaussian
MS	Measure of segregation; an index of the spatial segregation of the two populations along the gradient

rent for birth rates, death rates and competitive strength is not analyzed here.

II. Simulations: results and discussion

I analyzed two sets of simulation runs. In the first one the gradient was considered to be "infinitely flat"; that is, no environmental heterogeneity was taken into account. With this set of runs, the consequences of local dynamics alone on stability relations is explored (Section II.1). The concrete question to be answered is: How effective are local competition and limited propagule dispersion in stabilizing the coexistence of competing populations? The assumptions and conclusions of the Lotka-Volterra type competition models have been used as references for answering this question. (The structure of the simulation model justifies this choice of reference, c.f. Section I.2.).

With the second set of runs, the dynamical effects of environmental heterogeneity have been studied. The conditions of local competition and limited dispersion were in effect in this case as well, with the response curves having finite standard deviation parameters (σ—s) and distances of means (d values). Actually, with all other variables kept at constant values, σ—s and d—s were systematically changed within reasonable limits, and the tendencies for regional coexistence have been followed. Tendencies for random drift in the population abundances have been compared with and without response curves.

II.1. Local dynamics

To exclude marginal effects the opposite edges of the grid have been joined, thus forming a torus. This can be done only when response curves are not considered, as undesirable singularities would arise along the joining lines otherwise. In the simulations described in Section II.2., the edge effects could not be avoided this way, but the number of sites in the grid proved to be large enough to minimize the errors arising from this difference.

As there is no environmental gradient, $A_{ij}(\ell) = a_{ij}$ for all ℓ-s. Through 100 time units (t), the regional abundance of species 1, N_1 (t) ($N_1(t) = \sum_{m=1}^{1275} n_{1m}$) was recorded. (The abundance of species 2 can be calculated from this values as $N_2(t) = 1275{*}k - N_1(t)$, since the total number of individuals is 1275*k, when the grid is saturated.) Results:

(CASE 1.) Both local (within site) and regional (within grid) coexistence of the populations, if $a_{12} < 1$ and $a_{21} < 1$ (see Fig. 3a). This is the equivalent of the conclusion drawn from the Lotka-Volterra models in case of all populations being the strongest competitors of themselves.

(CASE 2.) Local exclusion, but regional coexistence, if $a_{12} = a_{21} > 1$ (see Fig. 3b). This means that all populations are equally strong competitors of each other, and intraspecific competition is less intense than interspecific. In this case, both populations aggregate into monodominant patches, from which they exclude the other species. These patches coexist within the grid (regional coexistence). This combination of parameters would lead to the complete exclusion of one or the other population in a Lotka-Volterra model. Which of the species wins would depend on the initial abundances. For our (and others, e.g. Weiner and Conte 1981) simulated case, increased tendency for coexistence arises from the local character of competition and dispersal, which

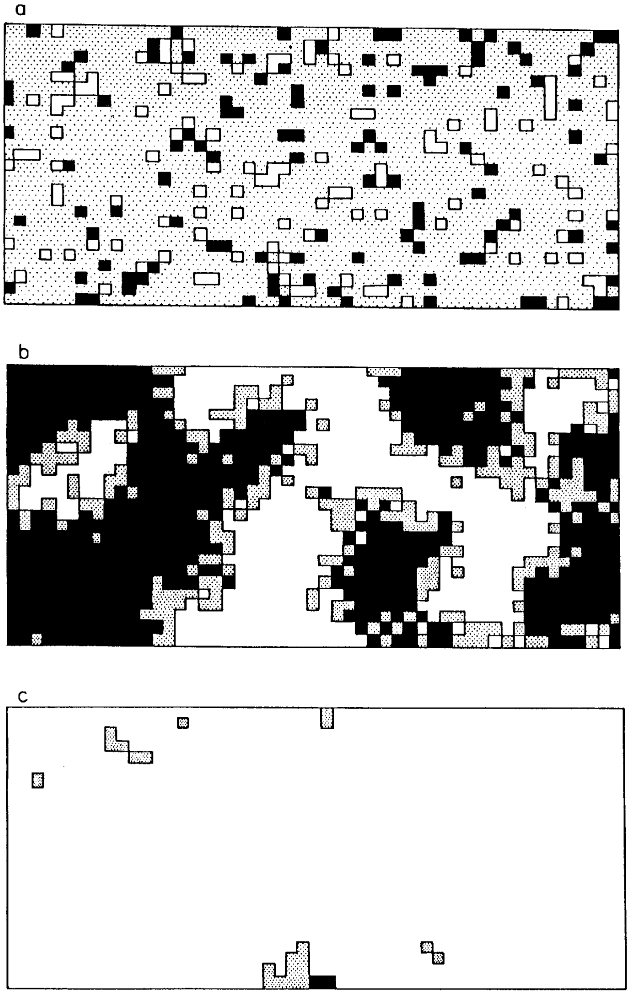

Fig. 3. Spatial patterns of the populations after 10 generations, without environmental gradient. Constants and legend:
$k = 3$, $f_i = 4$, $p_i = 0.6$, $N_i(0) = 1000$ ($i = 1,2$)
a) $a_{12} = a_{21} = 0.5$
b) $a_{12} = a_{21} = 2.0$
c) $a_{12} = 1.5$, $a_{21} = 2.0$
white: Sp. 1 present
black: Sp. 2 present
stippled: Sp. 1 and Sp. 2 present.

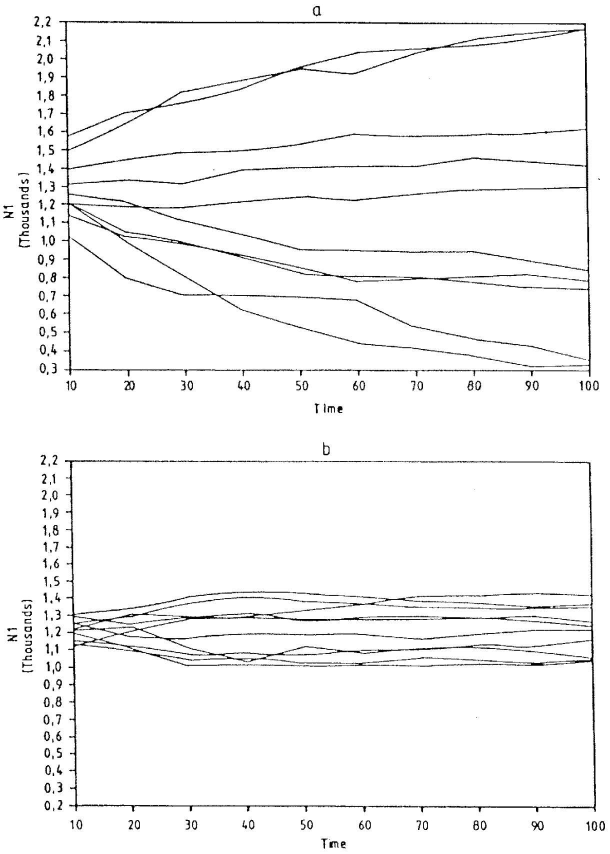

Fig. 4. Abundance of Sp. 1 in 10 runs, through 100 generations with $k = 2$, $f_i = 4$, $p_i = 0.6$, $n_i (0) = 1000$ $a_{ij} = 2.0$ ($i, j = 1,2$ $i \neq j$). The 10 runs within both graphs differ only in the initial values of the pseudo-random number generator
a) without environmental gradient ($d = 0$, $\sigma = \infty$)
b) $d = 16$, $\sigma = 40$.

is an assumption never included in ordinary differential equation models. However, Fig. 4a demonstrates that this tendency is not robust enough: the regional abundance of species 1, N_1 (t), is subject to random variation within broad limits, up to the possible point when the regional extinction of one of the species occurs. Which of the populations performs better is merely a matter of positional priority if the initial abundances are the same, and of abundance priority otherwise. All this means that the coexistence of the two populations is not maintained by any kind of regulative or directive forces, but only by stochastic effects which might easily induce extinction as well. In addition, we expect *CASE 2* not to arise very frequently in nature, since it requires the interspecific competition coefficients to be equal or very close, which is quite improbable for even similar species.

(CASE 3). Both local and regional exclusion, leading to the final victory of the stronger population, if $a_{12} > 1$, $a_{21} > 1$ and $a_{12} \neq a_{21}$ (see Fig. 3c and Fig. 8b). The Lotka-Volterra equations give the same outcome for this case.

Without the effect of an environmental gradient introduced, the local character of competition and dispersal leads to coexistence only in *CASE 2*, but not in *CASE 3*. Moreover, the coexistence in *CASE 2* is only a possibility; given enough time, exclusion might occur due to random drift. In *CASE 1*, coexistence is not tied to the local dynamical features, as it appears in the Lotka-Volterra models, without spatial constraints, as well.

Summarizing the above arguments, the local nature of population dynamical effects alone seem insufficient to ensure the coexistence of competing species, or if so, it is possible only in very specific cases. (Note that this statement applies to 2-species situations; if there are more populations, there is a possibility for their coexistence without the competition coefficients necessarily being equal. Competition must be a local interaction, and at least part of the competition matrix must form an "intransitive network" in this case - see Karlson and Jackson 1981 and Czárán 1984).

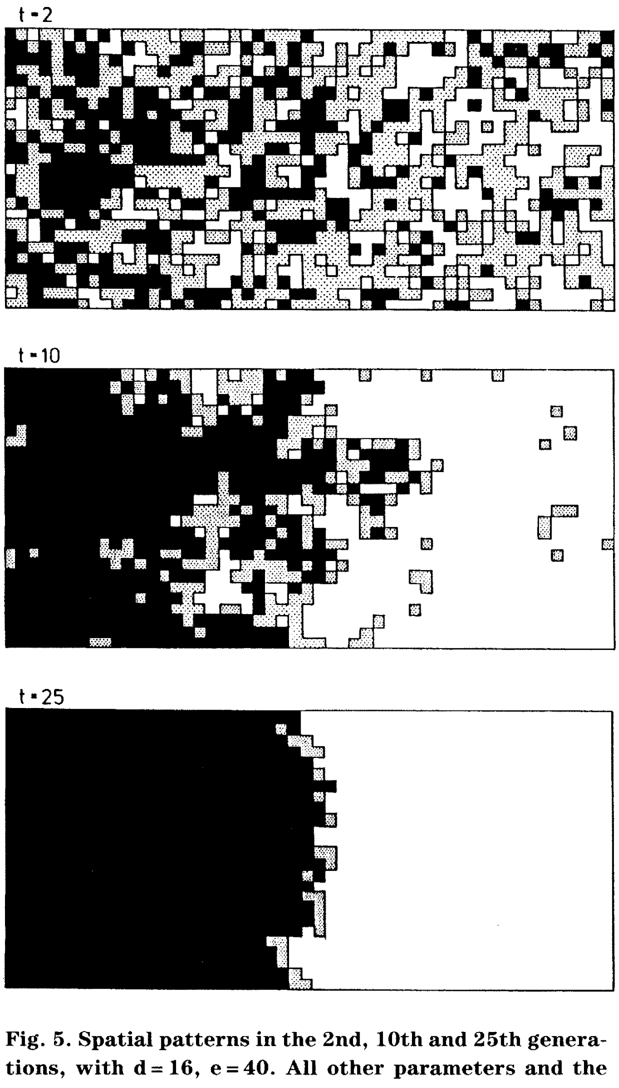

Fig. 5. Spatial patterns in the 2nd, 10th and 25th generations, with $d = 16$, $e = 40$. All other parameters and the symbols are like in Fig. 3b.

II.2. Environmental heterogeneity

If the response curves of two competing species are different enough (that is, their optimum points are quite far from each other, and the curves themselves are steep; as in Fig. 1), the regional coexistence of heavily competing populations is possible if the environmental variable to which the response curves regard shows a gradient sufficiently steep within the region studied. In this case, one of the species tends to win at one end of the gradient, the other will gain the other side, with quite a sharp boundary between the "territories" of the populations (see Fig. 5). It is much less easy to predict, however, how much the response curves should differ to ensure coexistence. To answer this question, it will be supposed that the competitive relations between the two species are the same as in *CASE 2* and *3* of Section II.1., and the distance (d) and steepness (σ) of the response curves change systematically.

(CASE 2'). As in CASE 2, fecundities and dispersal values are identical for the two species, and the optimum values of the interspecific competition coefficients are also supposed to be equal. d values range from 0 to 16 sites, σ-s from 40 to 100. Increasing steepness of the environmental gradient can be considered by decreasing σ values and/or increasing d values for the two populations. These two parameters could be jointly handled as d/σ (as done by May and MacArthur 1972, for utilization functions on a resource quality axis). This seems not be an appropriate method here, since it is not the product-integral of the curves - which is dependent on d/σ only - that defines the intensity of population interactions, but the individual combinations of parameters d and σ themselves. The null situation is characterized by $d = 0$; the response curves coincide in these cases.

A standardized index value, MS (Measure of Segregation), is used to measure the spatial segregation of the two populations along the gradient. MS is defined so that its value is 0 when both species are uniformly distributed over the grid (minimally segregated). Even in the null case, the stochastic character of patch formation (local exclusion) might cause MS to grow high above 0 because of the intraspecific aggregation of both populations, but this effect is accidental, generating high variation in the outcomes depending on the sequences of random numbers used. MS = 1.0 means maximal segregation along the gradient, that is, sites within a column of the grid are occupied by only one of the species as much as possible. With a gradient sufficiently steep, MS values approximate 1.0 quite quickly and consistently. Thus, if there is a number of runs with the same input data except for the random numbers used, the average to variance ratio of the MS values, E (MS)/var (MS), might be regarded as a measure of stable segregation for the pair of populations. With 5 replicate runs of 100 generations for each parameter sets, Fig. 7 plots the final values of this measure. Their consistent increase through 3 orders of magnitude with the

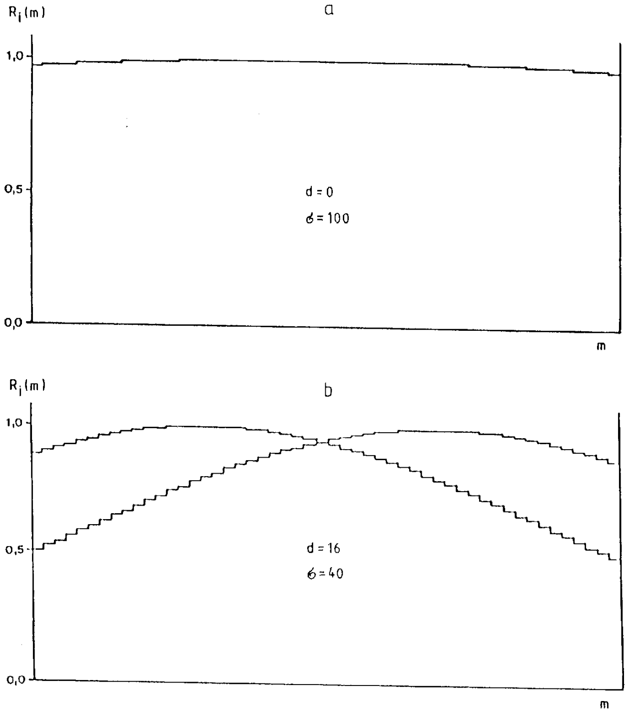

Fig. 6. The extremal configurations of response curves in the simulations resulting Fig. 7.

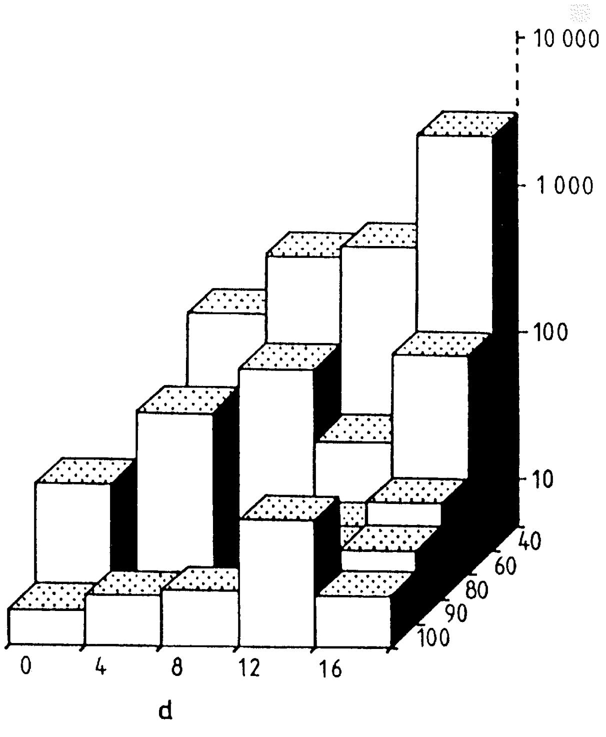

Fig. 7. E (MS)/var (MS), a measure of the stability of segregation along the gradient, for different values of d and σ. Constants: $k = 3$, $f_i = 4$, $p_i = 0.6$, $N_i(0) = 1000$, $a_{ij} = 2.0$ (i, j = 1, 2 $j \neq j$).

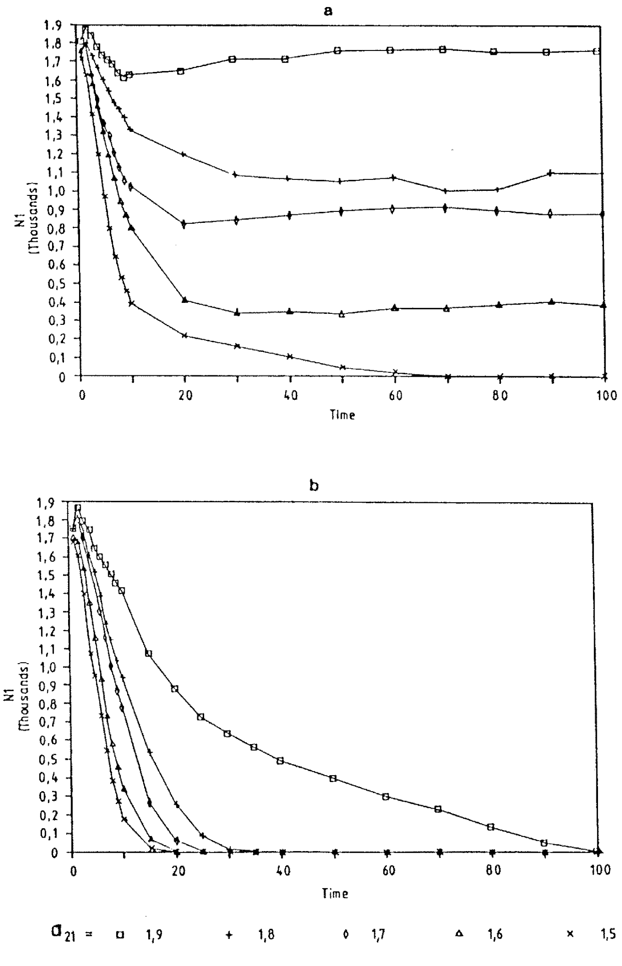

Fig. 8. Abundances of Sp. 1 through 100 generations, with different measures of competitive advantage for Sp. 2 Constant and legend: $k=3$, $f_i=4$, $p_i=0.6$, N_i $(0)=1000$, $a_{21}=2.0$ $(i=1,2)$
a) $d=16$, $\sigma=40$
b) without environmental gradient

steepness of the gradient growing demonstrates that stable regional coexistence through the division of space is possible even if a slight inhomogeneity of an environmental factor occurs. The response curves for the two extremal cases within the range considered ($d=0$, $\sigma=100$ and $d=16$, $\sigma=40$) are drawn in Fig. 6. The abundance ratio of the two species is also much more stable with the response curves slightly differing. Random drift effects can drive neither of the species to exclusion in this case; compare Fig. 4 a and b.

(CASE 3') As shown in Section II.1., a small difference between the interspecific competition coefficients of the two interacting populations is enough to generate the regional extinction of the weaker species, if they are similar otherwise, and no environmental heterogeneity is considered. The difference between the competition coefficients (a_{ij}—s) is the stabilizing force of the one-species equilibrium, as in the Lotka-Volterra models. However, this equilibrium can be shifted towards regional coexistence, by introducing the environmental gradient. To show this, Fig. 8a depicts the temporal changes of N_1, through 100 generations, with different values of the interspecific competition coefficients ($a_{12} \neq a_{21}$). The response curves are like in Fig. 6b in all cases. Fig. 8b shows the results without the gradient assumed, but with all other parameters kept unchanged. It can be seen that the measure of environmental inhomogeneity supposed by a small difference of the response curves is enough not only to stabilize the coexistence of species with the same competitive strength *(CASE 2')*, but to prevent exclusion despite the difference of the a_{ij}—s, up to the point where $a_{12}=2.0$ and $a_{21}=1.6$. It is not shown here, but easy to see intuitively, that more difference in competitive strength can be warded off by more difference of the response curves.

III. Conclusion

In two-species competitive situations with similar annual plant populations, the coexistence of the competitors is not guaranteed by the local manner of dispersion and competition alone. In fact, the smallest difference between the competition coefficients leads necessarily to the regional exclusion of one of the competitors. The stability of coexistence can be much enhanced by introducing a slight inhomogeneity of an environmental factor, that affects indirectly the competitive abilities of the populations. The gradient determines the direction along which the populations divide the region topographically, thus being able to coexist regionally, although excluding each other locally.

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